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ASSESSING FOREST RESPONSE-TYPE DIVERSITY TO NATURAL DISTURBANCES IN PENINSULAR SPAIN AND THE BALEARIC ISLANDS

Evaluación de la diversidad de tipos de respuesta a perturbaciones naturales en la España peninsular e Islas Baleares

MÁSTER EN INVESTIGACIÓN FORESTAL AVANZADA

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RESUMEN

Las perturbaciones afectan a los ecosistemas forestales influyendo en su composición, estructura y procesos. Para la cuenca mediterránea se prevé en un futuro próximo un aumento en la ocurrencia de eventos extremos de sequía, grandes incendios y – en menor medida – vendavales catastróficos. La estructura y funcionamiento de los ecosistemas forestales viene principalmente definida por las especies leñosas. La diversidad de respuestas frente a perturbaciones aparece como un buen indicador de la resiliencia ecológica. Con el objeto de avanzar en el conocimiento de la capacidad de respuesta de los bosques españoles a perturbaciones naturales se ha generado en este estudio una base de datos en la que se ha asignado para cada una de las especies que aparecen en el tercer Inventario Forestal Nacional (3IFN) la presencia o ausencia de nueve estrategias de respuesta asociados a la sequía, incendios y viento. La base de datos reflejó la falta de información existente para algunas estrategias de respuesta (especialmente para arbustos) y permitió determinar aquellos rasgos más frecuentes en las especies estudiadas. Con la información recogida se definió un índice relativo de resiliencia forestal a estas perturbaciones, calculado a partir de la abundancia de tipos de respuesta y la redundancia de especies para cada parcela del 3IFN en base a su composición arbórea y arbustiva. En general, pocas parcelas mostraron valores altos del índice de resiliencia, en parte porque algunos rasgos eran poco frecuentes y la mayoría de las parcelas presentaban muy pocas especies. La representación cartográfica del índice de resiliencia, mostró niveles bajos del mismo para las parcelas localizadas en sistemas montañosos, en los que dominan especies típicas de bosques centroeuropeos, mientras que las plantaciones gallegas de eucaliptos aparecían como uno de los sistemas más resilientes, reflejando la alta capacidad de estas especies para hacer frente a eventos más extremos de sequía, fuego y vientos. Se concluye que la base de datos puede convertirse en una herramienta muy útil para la gestión forestal y futuras investigaciones en la mejora de la resiliencia forestal.

Title: Assessing forest response-type diversity to natural disturbances in peninsular Spain and the Balearic Islands

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ABSTRACT

Disturbances shape forest ecosystems by influencing their composition, structure, and processes. In the Mediterranean Basin, changes in the disturbance regimes have been predicted to occur in the next future with a higher occurrence of extreme events of drought, wildfire, and – to a lesser extent – windstorm. Woody species are the main elements defining the structure and functioning of forest ecosystems. Recently, response-type diversity has been pointed out as an appropriate indicator of ecosystems resilience. For this, we have elaborated a complete response-trait database for the tree and shrubby species considered in the Third Spanish National Forest Inventory (3SNFI). In the database, the presence or absence of nine response traits associated to drought, fire, and wind were assigned to each species. The database reflected the lack of information about some important traits (in particular for shrubby species) and allowed to determine those traits most widely distributed. The information contained in the database was then used to assess a relative index of forest resilience to these disturbances calculated from the abundance of response traits and the species redundancy for each plot of the 3SNFI; considering both tree and shrubby species. In general, few plots showed high values of the resilience index, probably because some traits were scarcely presented in the species and also because most plots presented very few species. The cartographic representation of the index showed low values for the stands located in mountainous ranges, which are mostly composed by species typical from central Europe. In the other side, *Eucalyptus* plantations in Galicia appeared as one thee the most resilient ecosystems, due to its higher adaptive capacity to persist after the occurrence of drought, fire, and windstorm events. We conclude that the response traits database can constitute a useful tool for forest management and planning and for future research to enhance the forest resilience.

1. INTRODUCTION

Natural disturbances modify ecosystem structure and composition and, therefore, are key drivers of forest dynamics. In recent decades, changes in the disturbance regimes have been detected in the Mediterranean region (Schelhaas et al., 2003; Lloret et al., 2009) with a higher occurrence of high intensity events such as drought, wildfire, and intense storm episodes (Giorgi and Lionello, 2008). This increment is attributed in general to a combination of factors related to environmental and socio-economic changes (Alados et al., 2004; Ameztegui et al., 2010). Due to its particular location, in a climatic transition zone, the Mediterranean basin is known to be particularly vulnerable to these changes, which are expected to highly impact forest species and communities and the associated provision of desired ecosystems goods and services to society (Nocentini and Coll, 2012). Under this context of change, advancing in the understanding of the capacity of forests to respond to the occurrence of natural disturbances is of essential importance for the adequate definition of future forest management and planning strategies.

The resilience approach is concerned with how to persist through continuous development in the face of change (Folke, 2006). Since its origins in the seventies (Holling, 1973), resilience has been defined in numerous ways (for an overview of definitions see Brand and Jax, 2007). Recently, several authors have stressed the need of integrating resilience thinking in forest science (Benson and Garmestani, 2011; Puettmann, 2011; Rist and Moen, 2013). However, the ambiguity of the concept and the difficulties associated to its estimation difficult its practical application for forest management purposes (Rist and Moen, 2013). At forest stand-level, Puettman (2011) suggested that the quantification of the diversity of plant traits associated to ecosystem processes, and in particular to the ability of the ecosystem to respond to changes, would provide an adequate characterization of its resilience.

In the particular case of the Mediterranean region, plant-response traits are varied. For example, in areas exposed to intense summer drought many species present hard and thick sclerophyllous leaves or with down on their underside to avoid water loss (Cowling et al., 1996; Matesanz and Valladares, 2014). Other traits such as bark thickness, serotiny, heat-stimulated germination or post-fire seedling emergence are adaptations typically associated to fire disturbances (Keeley, 1986; van Mantgen and Schwartz, 2003; Paula et al., 2009; VanderWeide and Hartnett, 2011); whereas anemophily, anemochory or wood density are traits that may help plants to respond to windstorm events (Chave et al., 2009). There are also some plant traits that are important for the response of plants to more than one single

disturbance. For example, rooting development allows plants to reach moist at deeper levels in the ground, but also to anchor the plant in the ground in places highly exposed to wind (Valladares, 2004; Crow, 2005). Still, plants with long seed bank longevity could withstand drought periods and fires without serious damages in seeds (del Cacho et al., 2012; Paula et al., 2009); and resprouting ability let many plants to recover of physical damages due to drought, fire, windthrow or herbivory (Valladares, 2004; Paula et al., 2009; Catry et al., 2013; Nzunda et al., 2014).

Because compiling species response traits is a very time-intensive task, scarce morphological trait databases are readily available in the Mediterranean basin (Paula et al., 2009), despite being one of the most vulnerable regions and being considered as a biodiversity hotspot (Cowling et al., 1996).

In this study, we assumed that a forest system is resilient to a disturbance when it is able to persist or re-organize after such disturbance has occurred. Based on this principle, we conducted an analysis of the resilience of Spanish forests to the main natural abiotic disturbances (drought, forest fires, and –to a lesser extent– wind) using data from the Third Spanish National Forest Inventory (3SNFI) and bibliographic information about species plant traits. This was achieved by: *i)* creating a response traits database to the main woody forest species from the Iberian Peninsula; *ii)* for each SNFI plot, quantifying both an index of response traits abundance and another one of species redundancy and, from them, getting an approximation of forest resilience; *iii)* mapping the values of the resilience index calculated for each plot and for each natural abiotic disturbances when only tree species were considered and when both trees and shrubs were included.

2. MATERIAL AND METHODS

2.1. Study area and plant species

The study area covers an extension of 498,834 km^2, and includes all provinces of the peninsular Spain and the Balearic Islands. Most of the study area (80%) belongs to the Mediterranean bioclimatic region; whereas, approximately a 17% falls within the Atlantic region and the remaining 3% to areas with high mountains that belong to the Alpine region. The area considered in this work comprises a varied topography, with more than 6,000 km of coast, an extensive high plateau, and high mountain ranges reaching elevations higher than 3,000 meters in some peaks. In addition, the study area also contains a wide range of climatic conditions, with mean annual precipitation ranging from less than 300 mm (SE of the Iberian

Peninsula) to more than 2,200 mm (NW Navarra and SW Galicia), and mean annual temperature from 2.5 ºC in the Pyrenees to 17 ºC in some provinces of Andalusia (Agencia Estatal de Meteorología, 2011). The north-western quarter of the study area and some mountain ranges correspond in general to siliceous soils, whereas calcareous soils prevail in the rest of the area. Saline soils can also be common in the seaboard, even extending to some interior areas.

In which respects to vegetation composition, Peninsular Spain holds a wide range of plant species from Mediterranean, Atlantic and Alpine bioclimatic regions, adapted to different soil characteristics. The most abundant tree species belong to genus *Pinus* and *Quercus,* followed in importance by *Fagus sylvatica, Eucalyptus globulus* and *Castanea sativa.* On the other hand, *Rubus* sp., *Ulex* sp., *Cistus sp., Erica arborea* and *Quercus coccifera* are the most frequent taxa of shrubs.

Current vegetation distribution is considered to be not only the result of environmental heterogeneity, but also of different processes affecting forest composition at a range of spatial and temporal scales. These processes include geologic and climatic changes, the consequences of the long history of anthropic influence on the territory, as well as several natural disturbances (Blanco Castro et al., 1997). Currently, forest fires, drought, and – to a lesser extent – windthrow are the main natural abiotic disturbances with effects on the landscapes of the study area.

2.2. The Third Spanish National Forest Inventory as data source

The study is based on data from the Third Spanish National Forest Inventory (3SNFI) (Ministerio de Medio Ambiente, 1997-2007). The 3SNFI was carried out within a systematic sampling design in which permanent circular plots were located at the intersections of a 1x1 km UTM grid that fell inside forest and other woodlands. Among the available data, the 3SNFI provides information about tree and shrub species composition and abundance in each plot. Tree species composition at the plot level is determined by the number of trees and the basal area ($m^2 \cdot ha^{-1}$), whereas shrub abundance is expressed as a percentage of canopy cover.

We used a total of 84,757 plots distributed across the study area and including 205 woody taxa (138 tree species and 68 shrub taxa) that were phylogenetically dispersed across 93 genera, 21 families and 17 orders. We included in our study all tree species and those shrub taxa with height greater than 1 meter (following Font Quer, 1977). Smaller shrubs were

considered to present different ecological functions and accordingly were discarder from the analyses.

2.3. Selection of response traits and database

We selected a set of nine macroscopic response traits related to drought, fire and wind and with low or null intraspecific variation (Table 1). We only selected those traits for which information was available for most of the consulted species. This excluded categories such as physiological traits (*e.g.* resistance to embolism) or cytological traits (*e.g.* vessel features or stomata characteristics) that are currently not available for many of them.

In the relatively small cases where information about one of the selected traits was not available for some species, we assigned to them the average value of the same trait found for species of the same genus. With all the collected information, we generated a database in which the presence or absence of each response trait was assigned to each species or taxa (1 or 0).

Table 1: Selection of response traits to the main natural abiotic disturbances, criteria followed to decide if a species presented a trait, and consulted sources

Response trait	Disturbance	Criteria	Sources
Bark roughness	Fire	Wrinkled bark or with deep cracks, not detached	López González (2001); Ruiz de la Torre (2006)
Rooting depth	Drought Wind	Deeper than 1.5 m; reference considerations	Lemoine et al. (2001); Crow (2005); Ruiz de la Torre (2006); Serrada et al. (2008); Green (2009); Nicolescu et al. (2009)
Leaf indumentum	Drought	Down, hard and thick cuticle	López González (2001); Ruiz de la Torre (2006)
Anemophily	Wind	Gymnosperms or with catkins	López González (2001); Ruiz de la Torre (2006)
Anemochory	Wind	Fruits/seeds with dispersal elements	López González (2001); Ruiz de la Torre (2006); Paula et al. (2009); Paula and Pausas (2009)
Adaptation of seeds and fruits to fire	Fire	Serotinous cones, heat-stimulated germination, high post-fire seedling emergence	Paula et al. (2009); Paula and Pausas (2009)
Seed bank longevity	Drought Fire	Higher than 3 years (also between 1-5 years or less than 4 years)	Catalán Bachiller (1991); Kleyer et al. (2008); Paula et al. (2009); Paula and Pausas (2009)
Resprouting ability	Drought Fire Wind	Reference considerations	López González (2001); Ruiz de la Torre (2006); Serrada et al. (2008): Bagaria et al. (2009); Green (2009); Gómez-Manzanedo et al. (2009); Paula et al. (2009); Paula and Pausas

			(2009)
Wood density	Wind	Higher than 0.601 $g \cdot cm^{-3}$	Rodríguez et al. (2006); Chave et al. (2009); Zanne et al. (2009); Vilches-Casals and Correal-Mòdol (2013)

Below, we briefly explain the importance of these response traits to face natural abiotic disturbances and we describe the consulted sources to characterize each taxon, as well as the criteria we followed to decide whether or not a species had the response traits.

2.3.1. Bark roughness

Bark thickness is an important trait to deal with some kind of low or medium intensity fires (VanderWeide and Hartnett, 2011). A thick bark provides insulation, avoiding damages in cambium. Thus, species with a thick bark, as for example cork tree (*Quercus suber*), will have less tissue damages due to high temperatures than those with thin bark (*e.g. Fagus silvatica, Betula* spp.). To get this information for all the species we consulted botanic handbooks – mainly Ruiz de la Torre (2006) and López González (2001) – in which there is a description of bark characteristics. As the bark thickness can vary from a few millimetres to some centimetres depending on the species, we considered that a species had thick bark when it was wrinkled or with deep cracks, and when it did not detach in sheets or strips. In all species we took into account the bark in mature individuals, and in cases in which bark characteristics depended on the position in the plant (*e.g. Pinus sylvestris*), we defined bark roughness at the bottom part of the trunk because it is the most exposed to fires.

2.3.2. Rooting depth

Rooting development provides a considerable adaptive advantage to deal with drought and wind. Deep rooting, for example, allows plants to reach moist at deeper levels in the ground, therefore avoiding stress situations during drought periods. On the other hand, the more developed the roots, the more anchored the plants are in the ground and the greater their resistance to windthrow. To get the information about rooting depth, we used Ruiz de la Torre (2006) as the main reference, and we completed our database with other sources such as Crow (2005), Serrada et al (2008), the USDA Plants Compilation (Green, 2009), the Lorenz von Ehren's planning tips (http://lve-baumschule.de/en) and other published studies focused on particular groups of species (Lemoine et al., 2001; Nicolescu et al., 2009). Since root systems in most forest species do not reach deeper than 2 meters, and 80-90% of the roots grow in the upper 60 cm (Crow, 2005); a threshold of 1.5 m was considered to decide if a species had deep roots.

2.3.3. Leaf indumentum

Leaf indumentum is another important trait to deal with drought. Hard leaves with a high content in wax and lipids, as well as those with small down on their underside help plants to avoid water loss during drought periods and, therefore, make these species more resistant to them. Information about leaf surface was easy to find in botanical handbooks (Ruiz de la Torre, 2006; López González, 2001) so, all the species could be characterized according this trait. We considered a species as presenting this trait when leaves had any kind of down on their underside and/or when they were hard and with thick cuticle.

2.3.4. Anemophily

One of the most evident adaptations to wind is anemophily, *i.e.* wind pollination. Having small and bare flowers in a position of the plant exposed to wind is a considerable advantage to favour cross-pollination between different individuals and, thus, improve both genetic diversity and adaptive capacity. Anemophilous species were identifiable by consulting botanical handbooks, where flowers and inflorescences are explained in detail (Ruiz de la Torre, 2006; López González, 2001). All gymnosperm species in the study area were considered as anemophilous, as well as angiosperms with catkin inflorescences consisting of bare or pale unisexual flowers.

2.3.5. Anemochory

Anemochory is the process of dispersal of fruits and seeds by means of wind. Similarly to anemophily, anemochory is another advantageous adaptation to wind. Some species have seeds and fruits adapted to reach distant places from the parent trees with the help of wind. This adaptation let such species colonize new areas where their chances of survival can be improve. Like anemophily, anemochorous plants were identified in botanical handbooks (Ruiz de la Torre, 2006; López González, 2001). Nevertheless, we also consulted the BROT database (Paula et al., 2009; Paula and Pausas, 2009) to complete some data. We considered a species as anemochorous when its fruits or seeds had dispersal elements – such as pappus, wings, or resin vesicles – that increase the seed surface without a significant weight increase; or when they were minuscule.

2.3.6. Adaptation of seeds and fruits to fire

Some species in the Mediterranean region show seeds and fruits highly adapted to fire. Compared with other species without this trait, these species have a great competitive advantage to colonize burned lands and are even favoured to a certain extent by fire

occurrence. The BROT database (Paula et al., 2009; Paula and Pausas, 2009), that compiles plant traits related to plant persistence and regeneration after fire in the Mediterranean region, was especially useful to complete our database with this information. The criteria used to consider a species as presenting this trait were: the presence of serotinous cones, heat-stimulated germination or high post-fire seedling emergence. Species that were hardly ever exposed to fire did not have this trait.

2.3.7. Seed bank longevity

Seed bank longevity is another important trait to cope with drought and fire. Storing viable seeds for long time lets plant communities have a higher chance of colonizing the area after disturbance. Just as the adaptation of seeds and fruits to fire, seed bank longevity provides species with a considerable competitive advantage as compared with those without this trait. Information about this trait was mostly extracted from the BROT database (Paula et al., 2009; Paula and Pausas, 2009), although we also consulted a handbook about seeds of forest tree and shrub species (Catalán Bachiller, 1991) and, to a lesser extent, the LEDA trait database (Kleyer et al., 2008). We considered species as presenting this trait when their seeds were viable for at least 3 years or that were described as presenting seed longevity of less than 4 years or between 1 and 5 years. Although *Cupressus* seeds remained viable for a relative short period (between 2 and 4 years), we considered these species as presenting this trait because they have serotinous cones in which seeds are able to remain viable for 8 and even 15 years

2.3.8. Resprouting ability

The ability of resprouting after a disturbance provides plant species with a great competitive advantage to persist in the affected area and to readily occupy the space earlier than other competitors. Resprouting species have latent buds in roots or stumps that, thanks to the storages of reserves in roots or in the top parts of roots, are able to emerge after a physical damage keeping the same genetics. Most information associated to this trait was extracted from the BROT database (Paula et al., 2009; Paula and Pausas, 2009). Nevertheless, we also consulted botanical handbooks (Ruiz de la Torre, 2006; López González, 2001), the USDA Plants Compilation (Green, 2009), Serrada et al. (2008) and other specific published sources such as Bagaria et al. (2009) or Gómez-Manzanedo et al. (2009).

2.3.9. Wood density

Wood density is an important trait related to windthrow resistance. In order to gather information about wood density for the considered taxa, we used the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009), which is the largest wood density database to date. We also consulted punctually some other publications as Vilches-Casals and Correal-Mòdol (2013), Rodríguez et al. (2006) and the web page of the Ecological Flora of California project (http://ucjeps.berkeley.edu/efc/index.html). Unfortunately, we were just able to complete our database with wood density values for 131 of all the tree species. For the rest of the trees and in the case of most shrubs information about this trait was not available and then was left in blank. Since our data collection ranges from 0.284 to 0.913 $g \cdot cm^{-3}$ (oven dry mass/fresh volume), we decided to consider that wood was dense enough to provide for windthrow resistance from the third quartile value, which was 0.601 $g \cdot cm^{-3}$.

2.4. An approximation to resilience

In order to obtain an approximation of the response capacity of forest systems to the main natural abiotic disturbances (drought, fire, and wind) we considered in our analysis two components: (*i*) the aforementioned response traits in the stands, and (*ii*) the redundancy of species holding these traits and thus being able to response to each disturbance.

2.4.1. Response traits abundance

We calculated the response traits abundance (RTA) for the three considered disturbances (drought, fire and wind) at a NFI plot level by weighting the presence or absence of traits in a given species (associated to each disturbance) by the abundance of the species into the plot. Once this value obtained, we divided it by the total number of the potential response traits and the total species abundance in each plot in order to obtain a relative index ranging between 0 and 1. Thus, RTA was calculated as follows:

$$RTA = \frac{\sum_{j=1}^{m}\sum_{i=1}^{n} V_{ij} \cdot A_i}{m \cdot \sum_{i=1}^{n} A_i} \qquad \text{(eq. 1)}$$

where n is the number of species within the plot, m is the number of response traits considered, V_{ij} is the response trait value given to the species i for the disturbance j (1, if the species has the response trait; 0, if not), and A_i is the abundance of the species i within the plot, measured as basal area (trees) or canopy cover (shrubs).

We firstly calculated this index for each disturbance and considering separately trees and shrubs. Then, we made a ranking in which plots with a null value of RTA (in each disturbance) took a rank value equivalent to 0, and then as the index increased, the rank value increased one by one. Therefore, we obtained the same number of different ranking values as that of different RTA values. Finally, we standardized the rank values for each disturbance and vegetation type.

2.4.2. Species redundancy

We determined the species redundancy index (SR) for a given disturbance type as the number of species within a plot that present one or more response traits associated to that disturbance. As it was made in the case of the RTA index, we calculated the species redundancy index at the plot level for each disturbance and vegetation type (trees/shrubs). Then, plots were ranked and standardized following the procedure specified above.

2.4.3. An approximation to resilience using RTA and SR

We determined for each plot and disturbance type a proxy of forest resilience (hereafter *resilience index*) by combining the standardized ranking values calculated for RTA and SR.

In a first step, we obtained resilience indices based just on tree species information as the sum of the standardized ranking values of RTA and SR calculated previously (see eq. 2). For example, tree resilience to drought was assessed by calculating the abundance of response traits to drought of all tree species within each plot (see section 2.4.1) and the tree species redundancy based on traits associated with drought (section 2.4.2). All the study plots were then ranked based on both calculated variables and the obtained rank value (for each variable) was standardized (between 0 and 1) and summed. As we obtained values ranging from 0 to 2, a new standardization was made to get an index comprised between 0 and 1.

$$StRTA_{T,j} + StSR_{T,j} = RESIL_{T,j} \rightarrow StRESIL_{T,j} \qquad \text{(eq. 2)}$$

where $StRTA_{T,j}$ and $StSR_{T,j}$ are respectively the standardized plot ranking values of RTA and SR for trees (T) and disturbance j (j = drought, fire or wind), and $RESIL_{T,j}$ is the trees resilience index to disturbance j before the standardization (then, $StRESIL_{T,j}$).

In a second step, and once the resilience indices using exclusively tree species had been obtained, we added the information obtained for shrubs and calculated a community resilience index based on redundancy and response traits found in all woody species (trees and shrubs). This was made by summing the plot standardized ranking values of RTA and SR calculated

for shrubs and the ones obtained for trees (see eq. 3). Again, the results of this sum (which ranged from 0 to 4) were standardized.

$$\sum_{i=1}^{2} StRTA_{i,j} + \sum_{i=1}^{2} StSR_{i,j} = RESIL_{TS,j} \rightarrow StRESIL_{TS,j} \quad \text{(eq. 3)}$$

where *i* is the type of vegetation (*i* = trees or shrubs) and $RESIL_{TS,j}$ is the resilience index of all the woody species to disturbance *j* before the standardization (then, $StRESIL_{TS,j}$)

Finally, a global resilience index was calculated (putting all disturbances together) as the sum of standardized ranking values of RTA and SR calculated for each individual disturbance using tree (eq. 4) and woody species information (eq. 5).

$$\sum_{j=1}^{3} StRTA_{T,j} + \sum_{j=1}^{3} StSR_{T,j} = RESIL_{T,all} \rightarrow StRESIL_{T,all} \quad \text{(eq. 4)}$$

$$\sum_{i=1}^{2}\sum_{j=1}^{3} StRTA_{i,j} + \sum_{i=1}^{2}\sum_{j=1}^{3} StSR_{i,j} = RESIL_{TS,all} \rightarrow StRESIL_{TS,all} \quad \text{(eq. 5)}$$

where $RESIL_{T,all}$ and $RESIL_{TS,all}$ are respectively the resilience index of trees and all the woody species to all disturbances before the standardization (then $StRESIL_{T,all}$ and $StRESIL_{TS,all}$).

2.5. Mapping the forest systems resilience to natural abiotic disturbances

We made a set of eight maps with the calculated values of resilience index for each SNFI plots considering only tree composition and all the woody species. For each of both types of vegetation (just trees and trees and shrubs) we mapped separately their resilience indices to each disturbance, and then we did the same thing for all disturbance types combined. It is important to mention that the generated maps provide information about the relative resilience of a given SFNI plot with respect to the other plots, because these indices were calculated based on the ranked position of the plot in relation to all calculated RTA and SR values.

These maps were useful to identify the *a priori* most vulnerable areas to drought, fires and wind, as well as the most responsive (based on the criteria we used). On the other hand, by mapping separately plot resilience based on tree composition and the resilience based on all woody species (trees and shrubs), we could identify the zones where shrub species play a greater role in forest resilience.

3. RESULTS

3.1. Response traits database

In general, we found more information about response traits for trees (99.10% found traits for all the species) than for shrubs (78.33% found traits for all taxa). Whereas bark roughness,

leaf indumentum, and wind dispersal adaptations (anemophily and anemochory) were relatively easy to find, information about rooting depth and wood density were not available for an important number of species. In the case of shrubs, for example we could not find data about rooting depth and wood density for the 79.41% and 67.64% of the taxa respectively (see Table 2).

Table 2: Number and percentage of blank trait recordings depending on vegetation type

Response trait	**Tree species**		**Shrub taxa**	
Bark roughness	0	0.00%	0	0.00%
Rooting depth	3	2.17%	54	79.41%
Leaf indumentum	0	0.00%	0	0.00%
Anemophily	0	0.00%	0	0.00%
Anemochory	0	0.00%	0	0.00%
Adaptation of seeds and fruits to fire	0	0.00%	2	2.94%
Seed bank longevity	0	0.00%	4	5.88%
Resprouting ability	1	0.72%	3	4.41%
Wood density	7	5.07%	46	67.64%

Considering only the traits for which we had information, the ones that were held by most species (trees and shrubs) were the ability of resprouting, the leaf indumentum and the rooting depth. In contrast, whereas approximate a half of the tree species presented wind dispersal adaptations, less than a fifth of the shrubs presented these traits. Wood density and adaptations of seeds and fruits to fire were more common on shrub taxa than on tree species (see Figure 1).

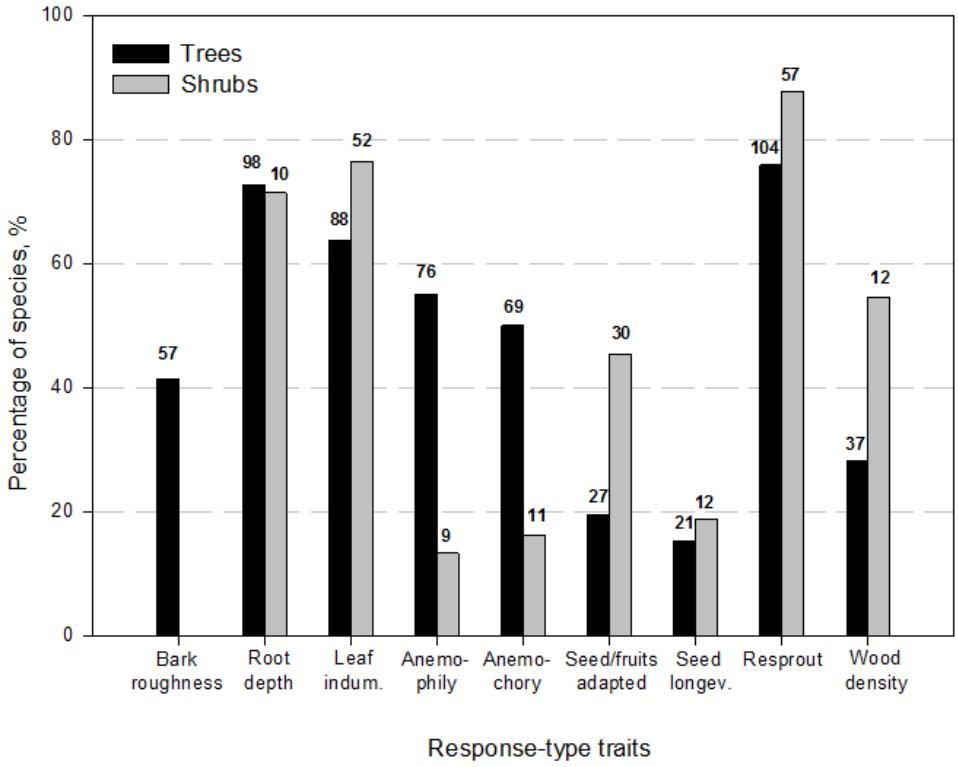

Figure 1: Percentage and number of tree and shrub species presenting each of the selected response-traits

3.2. Resilience indices

In general, we found that the presence of shrubs contributed to normalize the distribution of the RTA index within the studied plots. In addition, the percentage of plots with low values of SR was lower when we took into account all the woody species than when we considered just trees.

Values of resilience indices were differently distributed among plots depending on our consideration of either tree species or all the woody species together (trees and shrubs). In general, when we took into account all the woody species in the calculations there were more plots with higher values of the index than when considering only tree species.

3.2.1. RTA and SR indices

When we considered the tree species, around a half of the plots presented a RTA index to drought between 0.6 and 0.8 and only a 4.1% presented the highest values. The consideration of shrub species in the calculation led to normalize this index in such way that the percentage of plots with a RTA index between 0.6 and 0.8 decreased to approximately a tenth and the percentage of plots with lower and higher values increased in comparison with the percentage of plots when we considered just trees, especially those with the highest values (see Figure 2A).

In the case of the RTA index to fire calculated exclusively with tree composition, more than half of the plots presented values ranging between 0.4 and 0.6 and almost a third between 0.6 and 0.8, whereas the other value ranges were scarcely presented. Similarly to the RTA to drought, this index was more normalized when trees and shrubs were considered together. Thus, the percentage of plots with values between 0.4 and 0.8 were lower, increasing the percentage of plots with the other values of RTA (see Figure 2B).

Regarding to the RTA index to wind, approximately the 80% of the plots presented values between 0.4 and 0.8 when we took into account the tree species. The figure 2C shows that the consideration of shrubs together with trees normalized the RTA index. Thus, around a 50% of the plots presented values of RTA between 0.4 and 0.8 and lower and higher values were presented in a higher percentage of plots than without considering shrubs.

Finally when we took into account all the disturbances almost half of the plots presented a RTA index for trees ranging between 0.6 and 0.8 and only a 4.1% of the plots presented the highest values. Similarly to the case of drought, the consideration of shrubs together with trees led to decrease the percentage of plots with values ranging between 0.6 and 0.8 and increase the percentage of plots with the highest and intermediate values of RTA (see Figure 2D).

Regardless the type of disturbance, when we considered just trees the SR index took the lowest values for approximately 87% of the plots, for around a 11% of the plots this index ranged between 0.2 and 0.4 and hardly any plot presented a SR index higher than 0.4. The percentage of plots with the lowest values decreased to around 70 – 72% when we took into account trees and shrubs together depending on the disturbances and the percentage of plots with SR values between 0.2 and 0.4 increased to approximately the 25% (see figures 2E, F, G, and H).

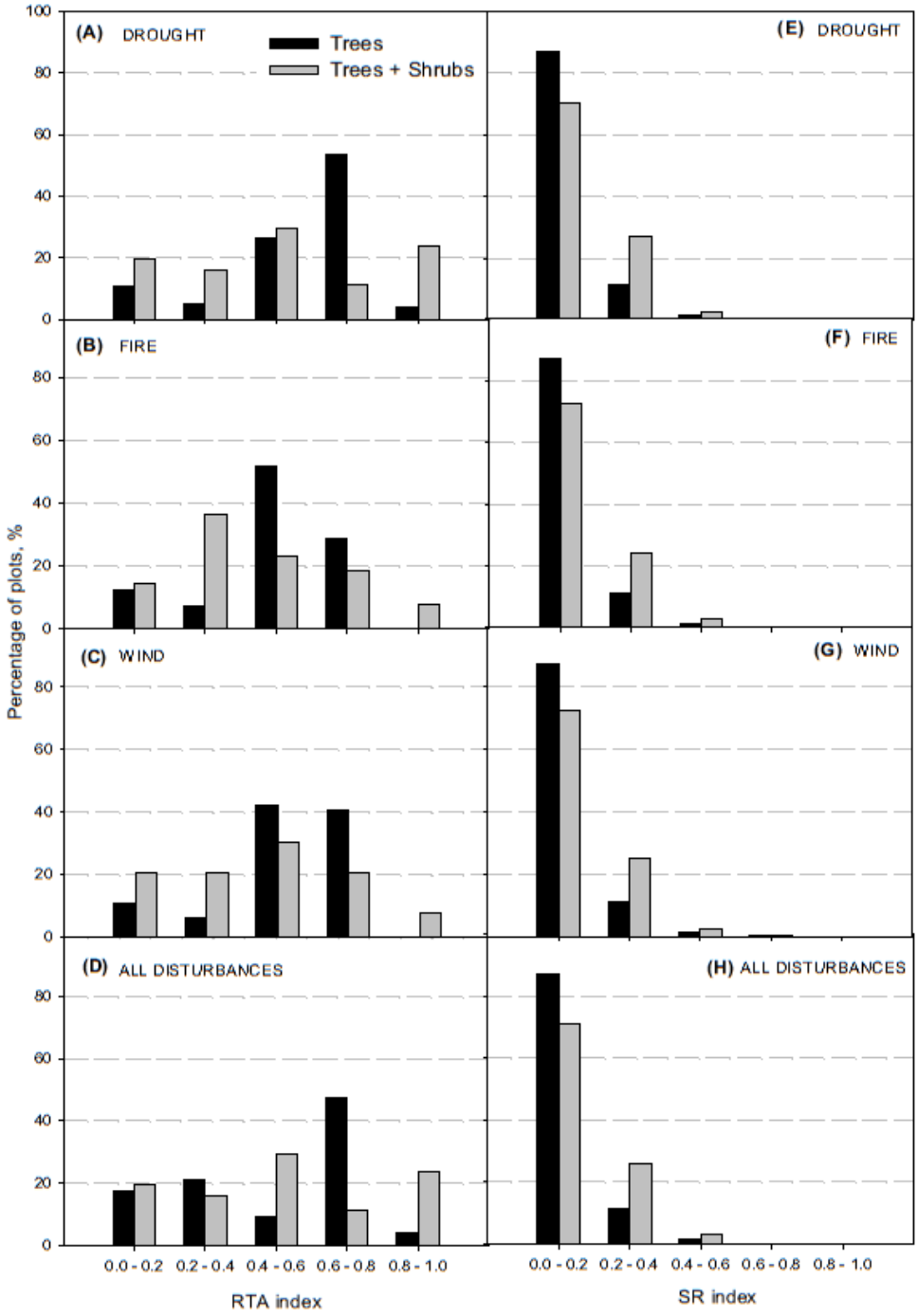

Figure 2: Distribution of plots among different values of RTA and SR indices to drought, fire, and wind for trees or for all the woody species.

3.2.2. Forest resilience to drought, fire, and wind

The 42.6% of the plots presented a tree resilience index to drought ranging between 0.4 and 0.6. For almost a third of the plots the index presented values below 0.2, and almost any plot showed a resilience index greater than 0.8. The consideration of all woody species, however, normalized the values of the resilience index to drought. Thus in contrast to the tree species resilience, there were fewer plots with low and intermediate values of the index, and the percentage of plots with higher resilience index was larger (see Figure 3A).

For approximately a half of the plots (52.1%) the values of the trees resilience index to fire were lower than 0.4, a 47% showed values between 0.4 and 0.8, and for hardly any plot (0.9%) the index was higher than 0.8. Again, shrub species contributed to normalize the resilience index. Thus, there were more plots with intermediate values than considering just trees (see Figure 3B).

Whereas the 60.8% of the plots presented a resilience index for tree species to wind lower than 0.4, considering trees and shrubs together there were 41.7% of the plots within this interval. The main difference between the resilience indices of both vegetation types was that for tree and shrub species there were more plots with intermediate values instead of the lowest (less than 0.4) and mid-high values (0.6 – 0.8). The highest index interval was a bit more represented (see Figure 3C).

In the case of tree species resilience to all the considered disturbances, almost a half of the plots comprised intermediate values of the resilience index (0.4 – 0.6), whereas the highest values of this index (0.8 – 1) were hardly presented in the study area. When we added the shrub species in the analyses, fewer plots presented the lowest and intermediate resilience values, but there was an increase in the percentage of plots with an index between 0.2 and 0.4 as well as in those with the highest indices (see Figure 3D).

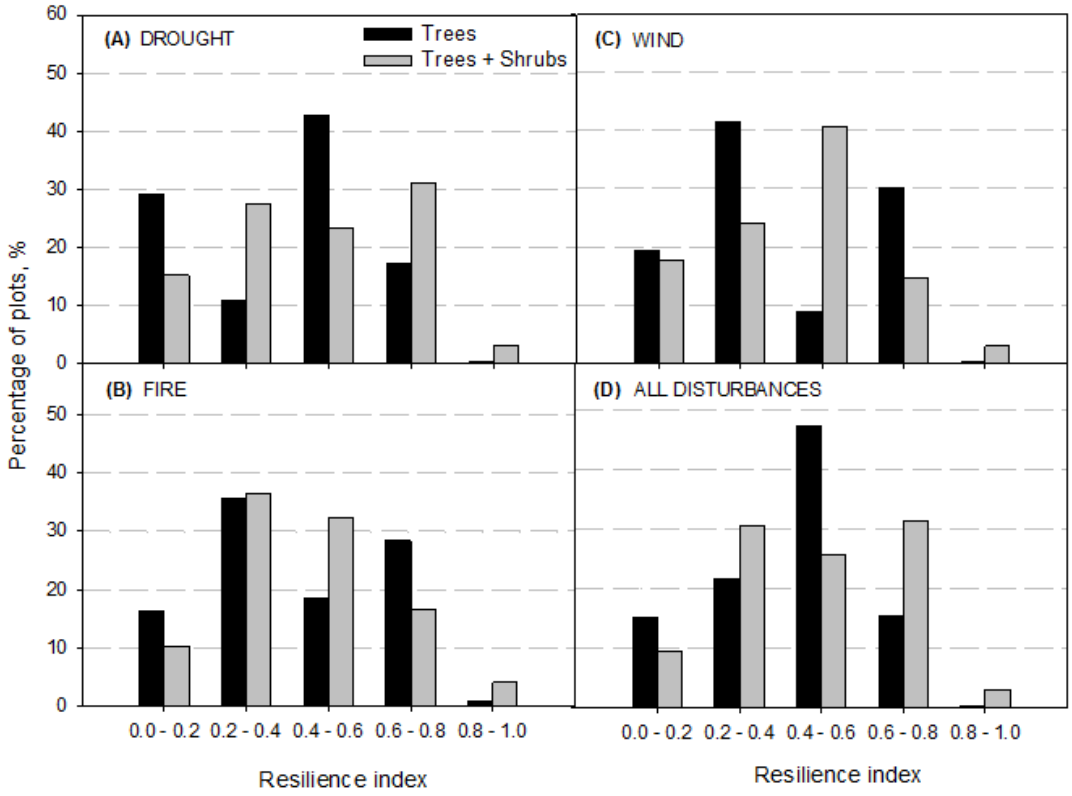

Figure 3: Distribution of plots among different values of the resilience index for trees and for all woody species to drought, fire, wind, and all natural disturbances together.

3.3. Cartographic representation of forest resilience to natural abiotic disturbances

3.3.1. Forest resilience to drought

According to the map of tree species resilience, the most vulnerable plots to drought were located along most of the highest mountain ranges (the Cantabrian Chain, the Pyrenees, the Iberian Chain and the Central Chain) and within the riparian forests in the north of the study area. In contrast, the most resilient plots (with a resilience index between 0.6 and 0.8) were found in the north-Eastern Mediterranean coast (Tarragona, Barcelona, Mallorca) and the western provinces of Galicia.

When the shrub taxa were considered in the computation of the index, there was a general increase in the number of the most resilient plots. Although some of the most vulnerable areas persisted – the Pyrenees, the south of the Iberian Chain, and the northern riparian forests – the rest of the study area presented moderate to high values of resilience to drought.

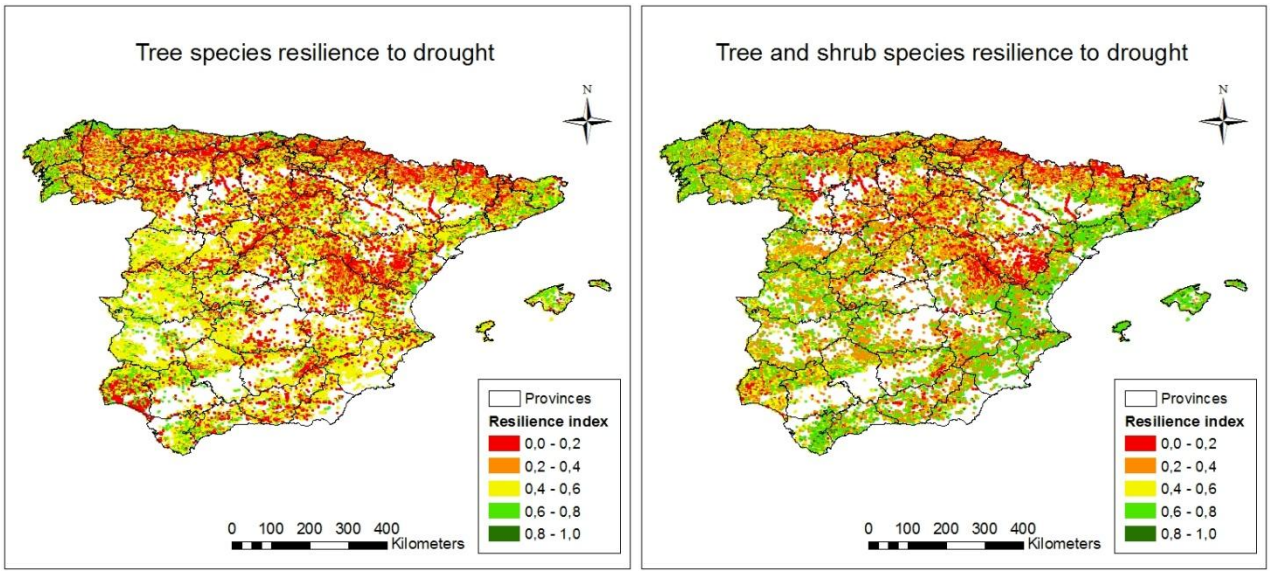

Figure 4: Maps of tree species (left) and tree and shrub species together (right) resilience to drought

3.3.2. Forest resilience to fire

The cartographic representation of tree species resilience to fire showed that, with the exception of the northwest and the east coast of Spain (both with a resilience index ranged from 0.6 to 1) and the Pyrenees (with intermediate values of resilience) the rest of the study area presented resilience indices lower than 0.4, being the Cantabrian Chain one of the most harmed areas among many other distributed by the rest of the area.

When the shrub taxa were included in the computations of the index, there was a slight improvement in the resilience of almost the whole area with the exception of the Pyrenees and the provinces of the Mediterranean coast.

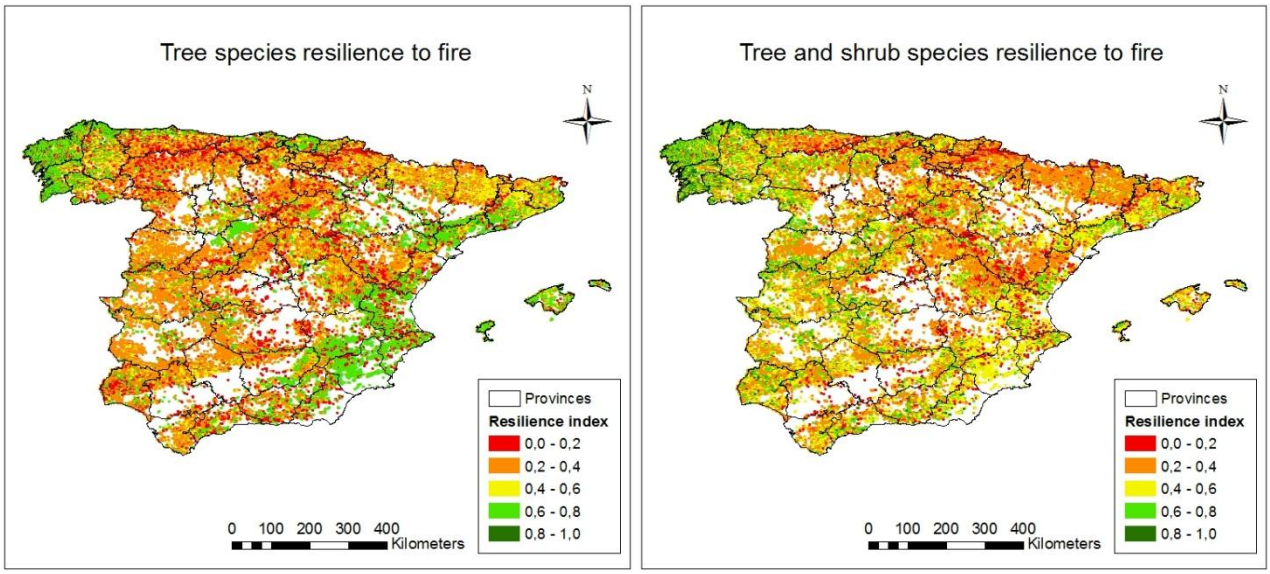

Figure 5: Maps of tree species (left) and tree and shrub species together (right) resilience to fire

3.3.3. Forest resilience to wind

According to the map of tree species resilience to wind, the most vulnerable areas were the north – excepting the Pyrenees, with intermediate values – and the east of the study area, as well as the Iberian and the Betic Chains. In general, the other areas presented resilience indices between 0.6 and 0.8.

In contrast to the other disturbances, the inclusion of shrub species in the forest resilience to wind did not improve the results. Whereas the mountain ranges and the interior areas showed a resilience index even lower than when we took into account just tree species composition, the coastal provinces presented greater values of this index.

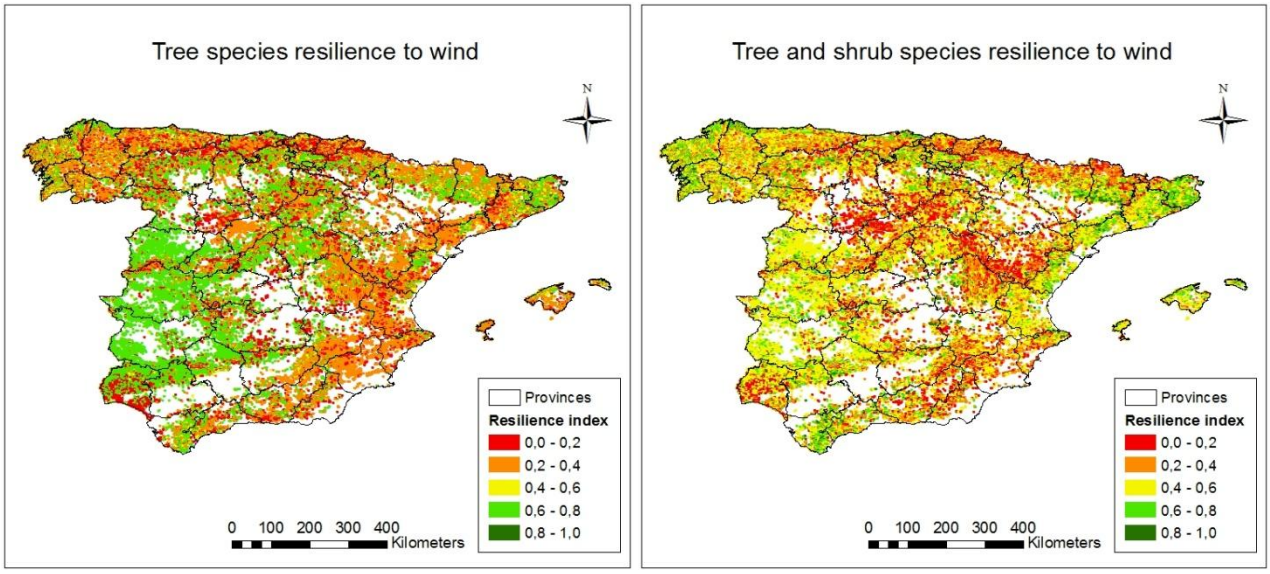

Figure 6: Maps of tree species (left) and tree and shrub species together (right) resilience to wind

3.3.4. Forest resilience to drought, fire, and wind

In general, global resilience for trees was intermediate for almost all provinces in the study area. The western provinces of Galicia stood out for having the highest resilience indices (0.6 – 0.8). Again, the Iberian Chain and, especially, the Cantabrian Chain and the north of Navarra were some of the less resilient areas.

With the consideration of both vegetation types, there was a general improvement in the global forest resilience. However, both the north of Navarra and the Iberian Chain did not improve their resilience index.

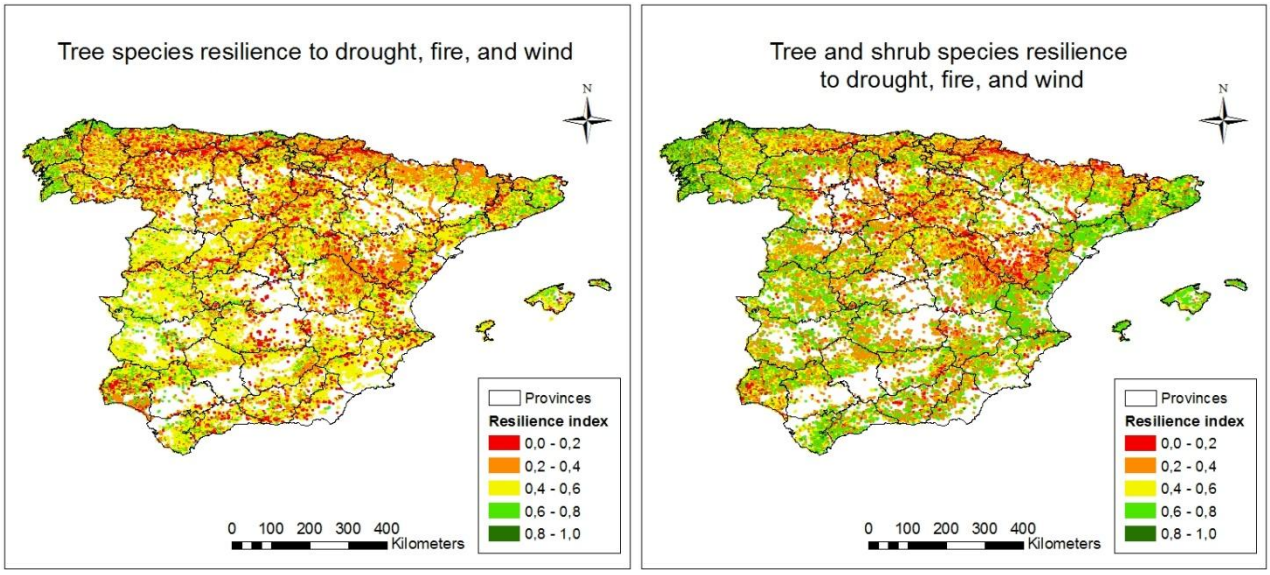

Figure 7: Maps of tree species (left) and tree and shrub species together (right) resilience to drought, fire, and wind

4. DISCUSSION

4.1. Response traits database

Information on plant traits is essential for understanding vegetation responses to disturbances and could be of great importance for defining adaptive directing management strategies in a context of increasing uncertainty. At present, great efforts are being done to compile as much information as possible about plant traits in many regions and ecosystems. Some of the most extensive databases include the LEDA database (Kleyer et al., 2008), the USDA Plants Compilation (Green, 2009), or the TRY plants trait database (Kattge et al., 2011). However, few of them are available for the Mediterranean Basin (but see Paula et al., 2009; Paula and Pausas, 2009; Bagaria et al., 2012). The database generated in this study will contribute to partially fill this gap. The database was created by compiling information about many woody Mediterranean species from an extensive literature review. Our compilation has

reflected the lack of knowledge that still exists about some important plant traits for many shrub species.

A first analysis of the database showed that the response traits more frequently present in forest species of Spain were the ones associated to drought (resprouting ability, rooting depth, and leaf indumentum); this reflecting the adaptation of most species in the study area to these type of events (Valladares et al., 2004; Sardans and Peñuelas, 2013). Nevertheless, the resprouting capacity is not just providing the capacity of responding to drought, but also with high levels of other natural disturbances, such as fires (Keeley, 1986) or wind (Nzunda et al., 2014). Response traits directly related to wind (anemophily and anemochory) seem to be more present in tree species than in shrubs, which is comprehensible due to their greater height. It is noticing that while most tree species with traits related to fire showed mechanisms to prevent fire damages (*e.g.* bark roughness); a large percentage of shrubs presented traits allowing them to recover after fire, such as adaptations of seeds and fruits to fire (Keeley 1986).

It is noteworthy to mention that the database we compiled has some limitations. The most important one is probably its binomial (*i.e.* presence/absence) character, which forced us in some cases (*e.g.* in the case of rooting depth, wood density) to define *a priori* thresholds or criteria to classify the species according to them. In addition, the database we generated was focused on macroscopic response traits and did not include other types of traits (*e.g.* physiological or cytological ones) or information of phenotypic plasticity which is known to play a major mode for adaptation of plants to changing environmental conditions (Matesanz and Valladares, 2014).

4.2. Resilience indices

4.2.1. The resilience index values in the study area

According to the results, few plots presented very high values of the resilience index. That was due to two fundamental causes: (1) for all the considered disturbances, there were always some response traits that were present for very few species (see Figure 1 in section 3.1); (2) approximate a fifth of the plots (17.5%) were monospecific, and the 62.7% of the plots had three or less species (considering both trees and shrubs). The absence of some of the response traits caused that very few plots presented RTA values higher than 0.8, whereas the low species richness made that almost any plot showed SR index higher than 0.6 (see Table 4

in Appendix A). Thus, because of the low values of both RTA and SR in most plots, the resilience index in the study area was in general lower than 0.8.

4.2.2. Potential limitations of the resilience index

The index we proposed to obtain an approximation of the forest resilience face to natural disturbances included both fundamental concepts of response diversity (measured by means of the *response traits abundance*, RTA) and ecological redundancy. Several studies have shown that response diversity is a better indicator of resilience than species richness and that both variables might not be correlated (Elmqvist et al., 2003; Chillo et al., 2011).

Although our index was very intuitive, easy to apply, and generally expressed the ability of forest plots to face abiotic disturbances, some counterintuitive results were also found. For example, a few plots having the same species redundancy and a lower average value of RTA than others presented a slightly greater value of resilience index. This probably reflects an artefact of the way in which the ranking was done, since we assigned the same increase rate regardless of the increase in the value of the sub-indices. On the other hand, it should be taken into account that all our indices are relative, *i.e.* the best plots according to the results are not necessarily very resilient to the considered disturbances but more resilient than most of other plots. On the contrary, plots with a low relative resilience index are less resilient than the others, but could still present some adaptive traits to respond to such disturbances.

In any case, in order to include the promotion of resilience in forest management, it will be essential to define a resilience index that allows an easy and intuitive diagnosis.

4.3. Forest resilience to natural abiotic disturbances in the study area

4.3.1. Forest resilience to drought

According to our results, drought was the disturbance for which more plots presented a low tree resilience index, often below 0.2. Maps showed that some of the most vulnerable communities to drought were located in mountain ranges where most common species did no present any response trait associated to this disturbance. Due to the fact that Mediterranean mountains acted as warm-wet refuge for many plants in past climatically-adverse periods (Bennett et al., 1991; Médail and Diadema, 2009; Magri, 2010), these areas are now partly occupied by temperate broadleaf forests and humid coniferous forests, with tree species native to central Europe (Scarascia-Mugnozza et al., 2000) which are not much adapted to face drought. In a recent study, Ruiz-Labourdette et al. (2013) already predicted considerable changes in the species composition of Mediterranean mountain ranges with an expansion of

perennial sclerophyllous species in detriment to species with higher hydric requirements, such as deciduous broadleaves and Eurosiberian conifers.

Our results showed that the inclusion of shrub species in the analyses significantly increased the resilience index in almost all the study area. This is explained not only because of increasing redundancy associated to higher specific diversity, but also because response traits associated to drought were much more present in shrub species than in trees (with the exception of rooting depth). In agreement with this result, Matías et al. (2012) found that shrub species were less affected by more severe drought than trees, which are extremely dependent on summer conditions.

Regardless the type of vegetation (trees or all woody species) riparian forests of Northern Spain also presented low resilience to drought. The phreatophic physiology of these species and associated low tolerance to drought have also been pointed for other regions (Tyree et al., 1994; Stella et al., 2013).

According to our diagnosis, the Northwest of Galicia is one of the most resilient areas to drought events. This is probably explained by the high presence of *Eucalyptus* plantations for pulp production. In fact, according to our classification criteria, *Eucalyptus* spp. are among the most resilient species to drought, fire, and wind disturbances. Merchant et al. (2009) stressed that not only morphological traits provide *Eucalyptus* spp. with drought resilience, but also some physiological traits, such as the presence of quercitol which confer them osmotic resilience against environmental stress.

In spite of the morphological adaptations in response to drought that most Mediterranean plants have acquired, the results of our study suggest that climatic change may have important consequences for future forest dynamics in the study. This might be traduced by: (*i*) a greater expansion of sclerophyllous trees and shrub species in detriment to communities currently growing in mountain ranges and by (*ii*) a higher vulnerability of riparian forests which may not be able to respond to increasing warming and drying processes.

4.3.2. Forest resilience to fire

For millennia, forest fires have been the most frequent disturbance in the Mediterranean landscapes, not only due to natural causes, but also as a consequence of human activities such as the widening of the grazing surface for livestock. Nevertheless, climate change, extreme weather events, and fuel accumulation due to land abandonment and fire suppression policy

have led to increased incidence and severity of large wildfires in the Mediterranean basin for the last 40 years (IPCC, 2014).

When we considered only tree species composition almost half of the plots presented low or very low resilience indices to fire, with the most resilient plots being concentrated in the Western plots of Galicia (again thanks to the presence of Eucalyptus, a taxon with great resilience to fire (Pekin et al., 2009; Catry et al., 2013)) and in the Eastern coast of the study area (Mediterranean coast).

When we included shrub composition in the analysis, most plots presented a higher resilience index than when just tree species were considered. Lloret et al. (2002) already suggested that resilience to fires might be higher in shrublands than in forests, which were expected to recover more slowly after a wildfire. Some plots in the Pyrenees and in the Eastern coast showed a lower resilience index when shrubs were incorporated in the analysis than when they were absent (*i.e.* when just tree composition was considered). This fact should not be interpreted as a decrease of the absolute resilience of the stands (which may not make sense) but to a decrease in the ranking position of these plots compared to others for which the presence of shrubs improve in a greater way their resilience to fire.

4.3.3. Forest resilience to wind

The most resilient areas in relation to wind were different depending if only trees, or both trees and shrubs, were considered. The zones for which the inclusion of shrubs species increased their resilience index were mainly located along the coasts. Even though wind is not a major disturbance – at least not as relevant in terms of damage as drought or fire – in the Mediterranean basin (Scarscia-Mugnozza, 2000; IPCC, 2014), coastal Spain is often affected by low-severity wind disturbances (http://atlaseolico.idae.es/). Although only a few shrub species presented some response traits to wind (anemophily 13.2%; and anemochory 16.2%), most shrub species with such traits are typical from the coasts.

4.3.4. Combined forest resilience to drought, fire, and wind

In Mediterranean environments plants are exposed to multiple and sometimes simultaneous abiotic stresses. Tolerance to these situations is expressed by means of complex physiological, anatomical and morphological adaptations (Matesanz and Valladares, 2014). Mittler (2006) for example, stated that we cannot estimate the responses of plants to a combination of disturbances from their responses to each different disturbance applied

individually and Valladares (2008) stressed the need of further understanding about how plants cope with simultaneous gradients of multiple abiotic factors.

The results of our analysis showed that tree species in the study area presented, in general, an intermediate value of resilience index to all the considered disturbances. When all woody species were considered (i.e. shrubby species were added), these "global" resilience indices tended to increase for most plots. The western provinces of Galicia stood out for being the most resilient areas, whereas the north mountainous ranges were the less resilient. It is clear that the abundance of *Eucalyptus* spp. in Galicia contributed to the high values of resilience observed in this region (although these forests are in general monoespecific and thus present low SR values). In the other side, the low resilience of northern mountain forests may be explained by the abundance of species typical from central European ecosystems that are often at the limit of their distribution in the study area and are not so well adapted to the main abiotic disturbances in the Mediterranean basin.

5. CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

In this study, we have generated an interesting database with information about most macroscopic morphological that modulate plant response to abiotic disturbances for main shrubs and trees growing in Peninsular Spain and Balearic Island. The database has the potential to contribute to both answering interesting research questions and to test the consequences of different forest management options for Spanish peninsular forests in terms of response capacity to abiotic natural disturbances resilience of the stands. However this database if somehow incomplete and would highly benefit of additional information about physiological and cytological traits as well as phenotypic plasticity indicators (still not available for many shrubby species).

Further methodological developments are also needed to develop a standardized resilience index that includes both response diversity and ecological redundancy and that would allow establishing comparisons across ecosystems.

A more deep understanding of forest resilience and how response traits contribute to it would also imply additional research to find out if there is any threshold in the RTA (or SR) values that could guarantee forest resilience. If such thresholds exist, it would mean that an increase in the number of responses (or in the redundancy) would not result in an increase in the overall resilience of the system. In the same way, estimated values of resilience may be different if species located at a certain distance from the studied plot had been considered. In

effect, landscape connectivity is essential to enhance the resilience of ecosystems to possible changes in disturbance regimes, since it lets communities increase their genetic and phenotypic variation and enhance the likelihood of population to persist or migrate to places with different environmental conditions (Gillson et al., 2013). However, despite their acknowledged importance, our study did not allow incorporating the spatial pattern of response traits or forest connectivity into our resilience indices.

In this study, we assessed for example the contribution of shrubs by comparing the resilience of plots with and without its presence. In the same way, it would be interesting to determine the differences in resilience between different types of forests (conifers versus broadleaves) or between different bioclimatic regions. Furthermore, an assessment of the temporal dynamics of forest resilience could also provide further understanding of how different processes that are recently affecting Spanish forests (land abandonment, densification, species substitution, disturbance regimes…) are modulating its ability to cope with disturbances. For example, a comparison of forest resilience indices between the third and fourth SNFI could be used to gain understanding on these processes.

In summary, in this study we have generated a new database that we think can become a useful tool to advance in the understanding about forest resilience in the Mediterranean region and to assess how resilience distributes across biomes, regions and forest types, among others. We have also provided a first diagnosis at national level of the most vulnerable areas to current disturbances. Advancing in the generation of this sort of information could be of high relevance for the design of future adaptive forest management and planning strategies.

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APPENDIX A

Table 4: Plots distribution among five intervals of the RTA and SR indices to each disturbance, considering only tree species or tree and shrub species

Disturbance	Index Values	**Plots (%)** (trees)			**Plots (%)** (trees and shrubs)		
		RTA	**SR**	**RESIL**	**RTA**	**SR**	**RESIL**
Drought	0.0 – 0.2	10.83	87.07	29.1	19.45	70.01	15.1
	0.2 – 0.4	5.22	11.33	10.8	16.00	27.09	27.5
	0.4 – 0.6	26.20	1.45	42.6	29.63	2.72	23.4
	0.6 – 0.8	53.60	0.14	17.3	11.14	0.17	31.0
	0.8 – 1.0	4.15	0.01	0.2	23.77	0.01	3.0
Fire	0.0 – 0.2	12.19	87.39	16.4	14.31	72.83	10.3
	0.2 – 0.4	7.21	10.99	35.6	36.31	23.97	36.5
	0.4 – 0.6	51.92	1.46	18.5	23.21	2.94	32.4
	0.6 – 0.8	28.6	0.15	28.5	18.54	0.24	16.7
	0.8 – 1.0	0.03	0.02	1.0	7.63	0.02	4.1
Wind	0.0 – 0.2	10.88	87.04	19.3	20.53	71.98	17.7
	0.2 – 0.4	6.09	11.32	41.5	20.79	25.20	24.0
	0.4 – 0.6	42.40	1.47	8.9	30.42	2.64	40.7
	0.6 – 0.8	40.63	0.15	30.1	20.52	0.17	14.7
	0.8 – 1.0	0.01	0.02	0.2	7.74	0.01	2.3
Drought Fire Wind	0.0 – 0.2	17.53	87.04	15.2	12.69	70.93	9.4
	0.2 – 0.4	21.21	11.32	21.7	21.30	25.98	30.6
	0.4 – 0.6	9.46	1.47	47.3	28.96	2.90	25.7
	0.6 – 0.8	47.70	0.15	15.5	27.64	0.18	31.2
	0.8 – 1.0	4.10	0.02	0.3	9.41	0.01	3.1

APPENDIX B

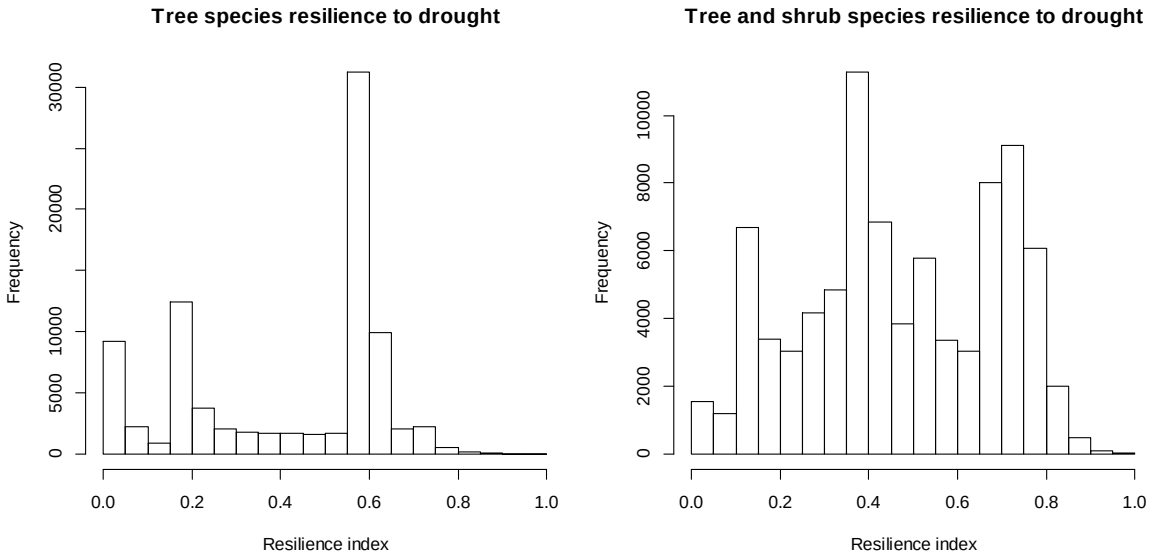

Figure 8: Frequency histograms of tree species (left) and tree and shrub species (right) resilience to drought

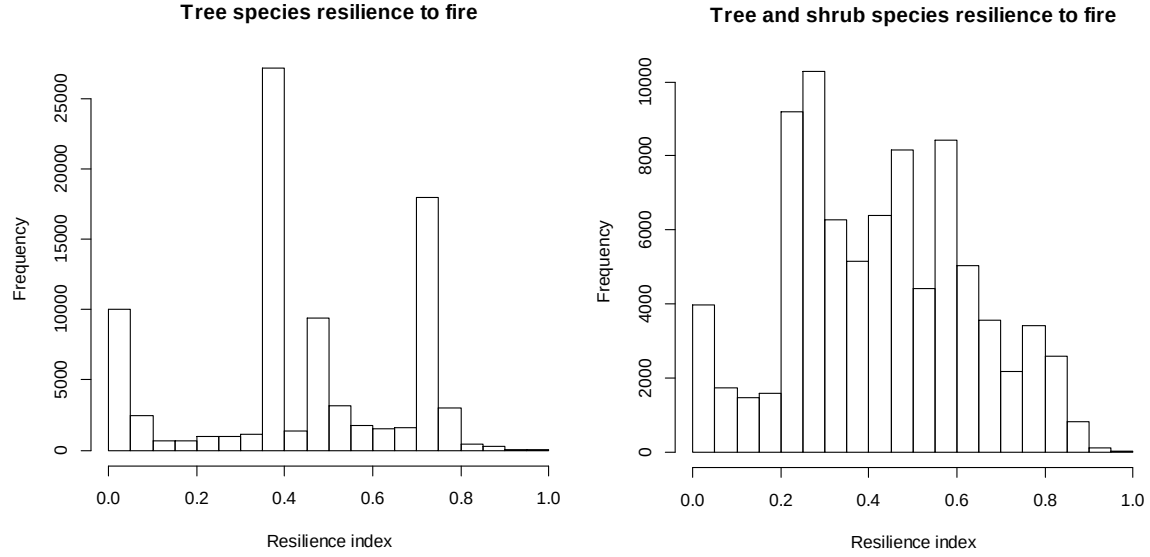

Figure 9: Frequency histograms of tree species (left) and tree and shrub species (right) resilience to fire

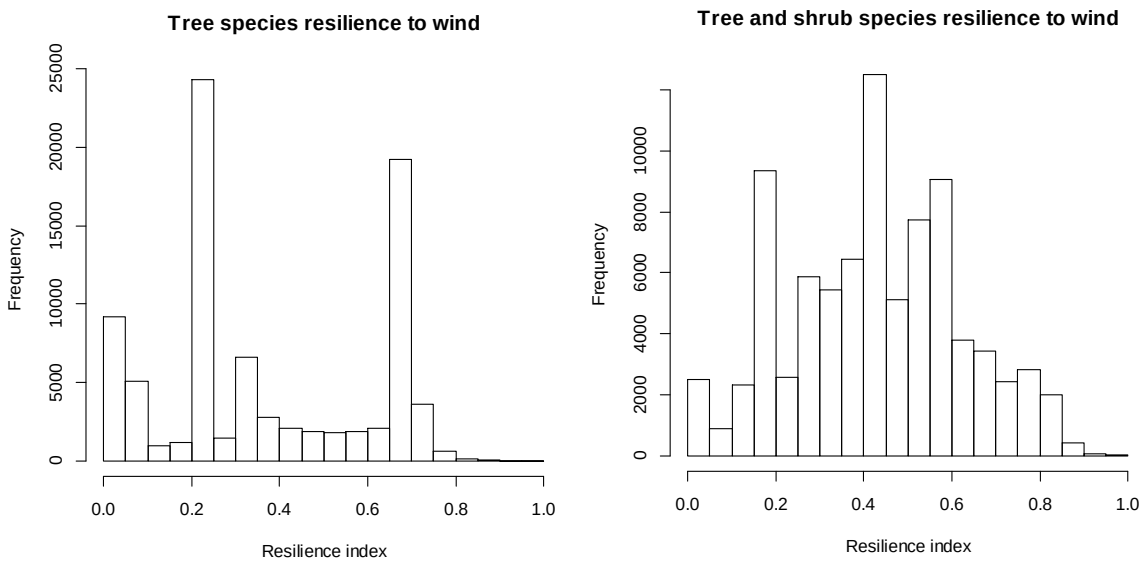

Figure 10: Frequency histograms of tree species (left) and tree and shrub species (right) resilience to wind

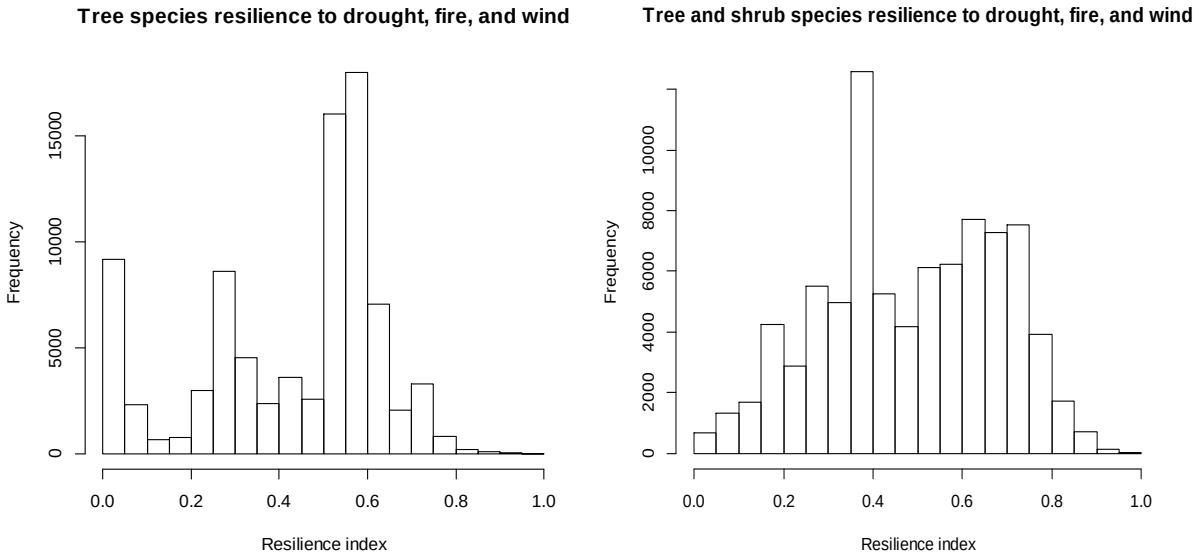

Figure 14: Frequency histograms of tree species (left) and tree and shrub species (right) resilience to drought, fire, and wind